BENTHIC MOLLUSCAN AND CRUSTACEAN COMMUNITIES IN LOUISIANA

by Douglas H. Farrell

ABSTRACT

This investigation examines species diversity, faunal similarities, and biomass relations of benthic communities in Timbalier Bay and offshore Louisiana. The bay and shelf regions were faunistically distinct with limited species exchange. Benthic fauna was temporally variable with many species apparently cyclic in occurrence. Seasonality was observed throughout the study area; maximum biomass and maximum species density occurred during spring. Biomass in the bay was not significantly different among different sites, but biomass of the shallow shelf was significantly higher than deeper offshore stations. A marked oxygen diminution occurred in the offshore region during July 1973 and was apparently limiting to biomass and most benthic species. The low dissolved oxygen levels apparently resulted from natural causes, probably the unusually high Mississippi River flood during the previous spring. Sampling was designed to examine possible long-term deleterious effects of oil platforms on the benthic environment, but no abnormal environmental stress could be attributed to the petroleum activity.

INTRODUCTION

Bordering the Gulf of Mexico, Louisiana contains 29,500 km^2 of

At the time of this investigation, Douglas Farrell was at the Department of Oceanography, Florida State University.

coastal marshes, which include about 13,700 km^2 of estuaries (Perret et al. 1971a). Extensive fisheries activities in these estuaries and on the adjacent continental shelf have resulted in Louisiana's position among the leading states in commercial fishery products—it is the leading producer on the Gulf. Louisiana tidelands and coastal waters support a multimillion dollar industry as well as thriving sports fishing activities, both of which depend on the "health" of coastal resources. Many commercial species use the estuaries and marshes as nursery grounds, and they migrate through the various biotopes of the estuary and shelf regions (Rounsefell 1966; McHugh 1966; Gunter 1967; Christmas 1973). Sport fisheries are not subject to regularly maintained statistics, but Gunter estimates that sport fishermen annually catch 100 million pounds or more of estuarine fishes in the Gulf. Despite the economic importance of the marine and estuarine resources of the Louisiana coast, most biological investigations have been limited to commercially important species. There is an obvious need for data on primary productivity, biomass, and marine and estuarine communities from the Louisiana coast.

Recent concern about pollution has prompted many investigations of marine resources around the United States. Perret (1971a) summarizes pollution sources in Louisiana from domestic and industrial wastes, dredging, and filling, but only briefly mentions petroleum industry activity. The impact of producing wells, associated petroleum industry activity, and long-term effects on the environment have only recently been studied (St. Amant 1971, 1972).

Timbalier Bay has been the subject of some biological study. The Louisiana Wildlife and Fisheries Commission emphasized the commercially important species in their assessment of Louisiana estuaries (Perret et al. 1971b). Waldron (1963), in the only benthic study, divided the bay into two biocoenoses based on distribution of Foraminifera. Several faunal studies of Louisiana were systematic in nature (Behre 1950; Causey 1953; Dawson 1966; Deichmann 1946; Harry 1942; Hoff 1943; Sprague 1950; and Willis 1942). Parker (1956, 1960) attempted to establish "faunal assemblages" on the distribution of living and dead mollusc shells.

My investigation was one aspect of a multi-discipline study of Timbalier Bay and the adjacent continental shelf. This region has been subject to active, sustained petroleum production for at least thirty years. The main objective of the present study was analysis of the epibenthic communities of estuary and shelf regions, with respect to petroleum industry activity and its long-term effect on benthic communities.

METHODS AND MATERIALS

Sampling methodology

Qualitative samples were collected with a small biological trawl (SBT). The triangular frame was fitted with a 505 mesh bag 2.4 m in length and 0.75 m on a leading edge. The trawl was towed for five minutes at a speed of one knot at selected stations. Quantitative samples were collected with a 1.5 m^2 Van Veen grab, which penetrated to at least 10 cm into the substrate.

All samples were washed aboard ship in a 505 sieve to reduce the size to a more easily handled bulk. Samples were then preserved in a 10% seawater formalin buffered with hexamethyleneamine and transported to the laboratory, where all benthic fauna were removed. The material was then sorted into major taxa and transferred to 70% isopropyl alcohol. Replicate Van Veen samples were collected whenever possible.

Sampling Stations

Before a comprehensive study of Timbalier Bay and offshore benthos could be initiated, an exploratory sampling program was necessary to delineate various biotopes and to define factors influencing distribution of benthic invertebrates in the area. Exploration began in August 1972 and concluded in October 1972, with pooled efforts of several investigators in a "biotope survey" of the near-shore region. Based on the surveys and historical data (Barrett et al. 1971a, 1971b), sampling sites were established in Timbalier Bay and adjacent near-shore regions (figure 1, table 1). Bay sampling stations were distributed over the general area with the principal experimental station near the Philo Brice platform (station 7) and the main control located near Wrong Name Pass (station 12). Selection of the control site was based on the lack of oil industry activity within the area and similarity to the platform site in substrate type and salinity range.

In the offshore region, producing platform 54A (see figure 1) was selected as the platform site. This platform is 25 km south of Timbalier Bay in about 20 m of water. Because of substrate differences, the control site used by the phytoplankton study and several other simultaneous investigations was unsatisfactory. However, one site examined during the biotope survey closely resembled the platform in substrate, depth, and fauna. This site was selected as the initial benthic control. Other sites located between the platform and shore were sampled whenever possible to obtain data for species exchange analysis. During July 1973, several

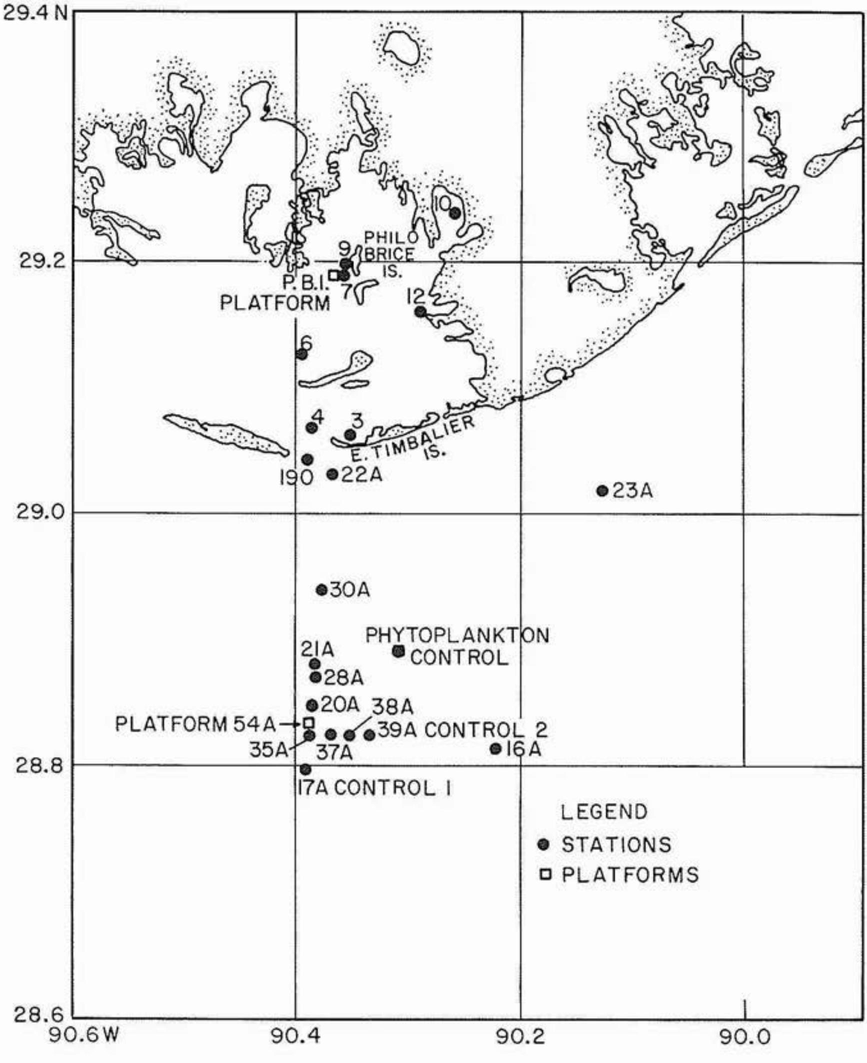

FIG. 1. STATION LOCATIONS IN TIMBALIER BAY, LOUISIANA, AND THE ADJACENT NEAR-SHORE REGION.

additional sampling stations were included as part of a cuttings survey in the area of the "oil well patch," and station 39A was retained as a second benthic control.

Analytical procedures

All crustacean and molluscan species were determined to the lowest possible taxon.

Table 1. General physical characteristics, location and sampling data for Timbalier Bay and nearshore stations, nearshore stations indicated by "A" following station number. Van Veen samples indicated by "x"; small biological trawl samples indicated by "y".

Station Number	Depth (m)	Bottom Salinity range o/oo	Substrate % sand/% mud	N. Latitude W. Longitude	Sampling Dates F72	W73	Sp73	Su73	F73	S74
3	1.7	24.8-29.3	95.2/4.6	29°03.72' 90°21.26'	y	x	x	x		
4	1.2	26.2-34.8	99.7/0.2	29°04.16' 90°23.35'		x	xy	x		y
6	1.6	18.3-27.3	39.0/60.7	29°07.59' 90°23.96'		x	x	x	x	
7 (Platform)	2.0	15.1-26.8	18.8/71.6	29°11.47' 90°21.62'		x	xy	x	x	y
9	1.2	13.4-19.0	35.3/53.5	29°11.88' 90°21.43'		x	x	x		
10	1.6	10.2-17.4	4.4/93.8	29°14.50' 90°15.50'		x	x	x	x	
12 (Control	1.8	17.1-33.3	18.3/81.5	29°09.70' 90°17.50'		x	xy	x	x	y
190	3.0	31.8	- -	29°02.60' 90°23.50'	xy					
16A	25.6	-	66.3/32.9	28°49.00' 90°13.30'	x					
17A (Control)	18.6	31.4-36.1	98.9/1.1	28°47.97' 90°23.58'	x	x	xy	x	y	xy
20A	20.1	31.2	49.6/50.2	28°49.96' 90°23.41'	x					
21A	18.7	30.7	34.3/64.9	28°52.90' 90°23.05'	x					
22A	5.1	23.9-35.7	82.2/17.4	29°01.90' 90°22.18'	x	x	xy	x	x	xy
28A	14.1	34.2-34.7	33.7/66.3	28°50.44' 90°23.14'			x		x	
30A	14.3	33.2-36.1	7.9/92.1	28°56.42' 90°22.73'			x	y	x	
35A (Platform)	20.1	31.2-36.1	97.0/2.9	28°49.96' 90°23.41'	x	x	xy	x	x	xy
37A	19.6	35.4	55.2/44.7	28°49.83' 90°22.30'				x	x	
38A	19.4	35.2	82.2/17.4	28°49.75' 90°21.18'				x	x	
39A (Control #2)	20.0	28.2-35.1	85.6/14.3	28°49.67' 90°20.06'				x	x	xy
Phytoplankton Control	20.1	34.73	12.8/72.2	28°53.5' 90°18.5'	y					

Biomass (wet weight) of benthic fauna, exclusive of meiofauna, was measured by volumetric displacement techniques for smaller specimens and direct weighing for larger organisms. For the Mollusca, correction factors were determined for the shell.

Species diversity was defined according to the methods of Shannon and Weaver (1963). The Basharin (1959) correction for sample size was included, and Pielou's (1966) "evenness" (J') component was also calculated.

The Wilhm (1967) modification of the Shannon-Weaver formula was used to determine biomass diversity. Faunal affinities between pairs of stations and samples were quantified with the Morisita (1959) index of similarity. Both the standard method and nonparametric applications of the similarity index are used to compare stations and biotopes.

Benthic biomass from the Van Veen samples was examined using two different designs of analysis of variance (ANOV). A two-way design ANOV was used on bay samples with seasons and stations as sources of variations, and a factorial two-way design was used for offshore biomass data.

Water quality data for Timbalier Bay stations and logistical support for bay work were furnished by Gulf South Research Institute (GSRI). Substrate samples were collected in cooperation with GSRI for interstitial nutrient analysis. Hydrography, water mass data, and logistical support for offshore collections were furnished by Southwest Research Institute (SWRI). Additional offshore support during September 1972 and July 1973 was furnished by the R/V *Longhorn,* The University of Texas. Most of the data on substrate type and distribution were furnished by Dr. J. I. Jones and Mr. Sam Williams. Total carbon and organic carbon substrate data for benthic stations were furnished by Dr. Charles Brent.

RESULTS

Data on physical parameters were normally taken from instantaneous measurements at time of sampling, and range of variation of these parameters between sampling periods is unknown. Sampling was based on quarter-annual intervals, and measurements presented here should approach seasonal variation. Unless otherwise noted, values of temperature, salinity, and dissolved oxygen represent bottom measurements and were collected as near the bottom as possible, depending on height of surface waves.

Salinity

The bay is a shallow (1-2 m depth), semi-enclosed basin with no major input of fresh water. Mean bottom salinities at bay stations ranged from 14.4 ppt at Little Lake (station 10) to 29.0 ppt near East Timbalier Pass (station 4), and mean bottom salinites at the platform and control sites were 20.5 ppt and 23.9 ppt, respectively. Station 22A near East Timbalier Pass exhibited the greatest range in salinity among near-shore stations (23.9-35.7 ppt). Salinities increased seaward and were most stable at station 17A (31.7-36.1 ppt). Salinities of bottom water at deeper stations were lowest when there was evidence of mixing between bottom and surface waters, during fall 1972.

Dissolved oxygen

Within the bay, dissolved oxygen (DO) levels followed a predictable pattern, with a maximum of 11.3 mg/l observed during February 1973 and a minimum of 3.6 mg/l occurring in July 1973. Dissolved oxygen in bottom water of near-shore stations reached a mean high of 7.3 mg/l during January 1973 and a mean low of 1.4 mg/l during July 1973. The low DO readings were apparently affecting the entire offshore study area during July sampling, and at some stations bottom water DO measurements as low as 0.05 mg/l were recorded. Fish kills were observed during this period. Although quantification was not possible, large numbers of dead, floating fish were seen at station 22A on July 11 and in East Timbalier Pass near bay station 4 on July 16. Seven of the fish at the bay site were identified as the Gulf menhaden *Brevoortia patronus*. Timbalier Bay apparently was not affected by this phenomenon. DO levels remained comparatively high and the two sampling sites nearest the bay mouth, stations 3 and 4, had DO levels of 7.4 mg/l and 8.0 mg/l respectively.

Temperature

While bay temperatures showed great seasonal variation, there was little difference among stations. Average bottom temperatures varied from 12.7° C in February 1973 to 29.0° C during July 1973. Among the near-shore stations, the shallowest, 22A, had the greatest seasonal variation in temperature (13.9° C - 24.2° C), and the offshore platform station, 35A, showed the least variation with a minimum of 19.0° C during February 1973 and a maximum of 24.9° C during July 1973.

Sediments

General substrate types are given in table 1. Bay stations ranged from nearly pure sand (99.65%) at station 4 to the very muddy sediments (93.83%) at station 10 in Little Lake. The platform station and control site in the bay both had sandy mud substrates. Among the offshore stations, the platform station and the controls had predominantly sandy bottoms, as did the station nearest to shore (22A). Intervening stations (20A, 21A, 28A, 30A), as well as the phytoplankton control station, were predominantly mud. With the exception of offshore platform station 35, total carbon content was correlated with mud content of the substrate. Only bay platform station 7 had an inorganic carbon level (1.69 mg/g) higher than 1.0 mg/g. Organic carbon content ranged from 0.26 mg/g at bay station 7 to 19.00 mg/g at bay station 10.

Other physical factors

Currents in the bay appeared to be tidal and reached noticeable velocities only in the passes. Southwest Research Institute reports wind, tides, and regional Gulf of Mexico currents as primary driving forces of currents in the offshore sampling area. Direction of bottom currents appears to be seasonal, and net transport was to the northwest, with an average velocity of 0.21 knots. I observed high turbidity of the bottom water in the form of a "turbid layer," as did other members of a diving crew in the near-shore area. Presence of the layer was confirmed by ship's transmissivity readings, and continued examination proved the layer to be temporally and spatially variable, reaching an apparent maximum density in April 1973. Griffin and Ripy (1974) reported the apparent source of the turbidity as the Mississippi River and not the existent substrate in the sampling area.

BIOLOGICAL RESULTS

Twenty-six Van Veen samples and 8 SBT samples were collected from the eight Timbalier Bay stations, and 58 Van Veen samples and 9 SBT samples from 12 sites were collected offshore (figure 1). Sampling was concentrated at stations 35A (platform 54A), 17A (benthic control 1), and 22A throughout the sampling phase. Station 39A (benthic control 2) was included during the second year. Samples were collected from other stations to furnish data from different biotopes whenever time permitted.

One hundred and one species of epibenthic molluscs and crustaceans were collected from the bay and offshore waters (tables 2 and 3). Crustaceans numbered 65 species, including 39 species of decapods, 19 amphipods, 4 cumaceans, 3 isopods, and 1 each of stomatopods and tanaids. There were 22 species of pelecypods and 14 gastropods. All groups were more numerous in terms of number of species offshore, where 78 species were taken compared to 55 from the bay.

There was little evidence of sessile flora or fauna at any of the sampling stations. The lack of vegetation apparently resulted from the high turbidity of the bottom water, which reduced the penetration of light at the bottom, and from the general lack of solid substratum. One bay SBT haul contained several small pieces of a benthic green alga, which probably originated from the vicinity of Casse-tete and adjacent islands. At stations 17A, 35A, and 39A occasional small pieces of branching ectoprocts were collected, usually attached to worm tubes.

TABLE 2. Species list of epibenthic invertebrates collected in Timbalier Bay and Offshore Louisiana, 1972-1974.

	Bay	Offshore
Phylum Mollusca		
Class Gastropoda		
Anachis avara		X
A. obesa	X	
Cantharus cancellarus		X
Epitonium krebsi		X
E. rupiola	X	
Murex fulvescens		X
Nassarius acutus	X	X
N. vibex	X	X
Olivia sayana		X
Polinices duplicatus	X	X
Sinum perspectivum		X
Terebra dislocata	X	X
Thais haemastoma	X	
Turbonilla sp.		X
Class Pelecypoda		
Argopecten irradians		X
Anadonta ovalis	X	
A. transversa	X	X
Chione cancellata		X
C. grus		X
C. clenchi		X
Corbula sp.		X
Diplodonta punctata	X	X
Docinus discus	X	
Donax tumidus	X	
Ensis minor	X	
Macoma sp.	X	
M. mitchelli	X	
Mercenaria campechiensis	X	X
Mulina lateralis	X	X
Noetia ponderosa		X
Nucula proxima		X
Nuculuna concentrica	X	X
Solen viridis		X
Tellidora cristata	X	
Tellina alternatis	X	
T. iris	X	X
Phylum Arthropoda		
Class Crustacea		
Order Stomatopoda		
Squilla empusa	X	X
Order Cumacea		
Cyclaspis sp.	X	X
Eudorella monodon	X	
Leucon sp.	X	
Oxyurostylis smithi	X	X
Order Tanaidacea		
Leptochelia sp.		X
Order Isopoda		
Ancinus depressus	X	X
Edotea montosa	X	X

(continued next page)

Munna sp.		X
Order Amphipoda		
Acanthohaustoruis sp.	X	
Ampelisca holmesi	X	X
A. vadorum		X
Batea catharinensis	X	X
Caprella sp.		X
Cerapus tubularis		X
Corophium acherusicum	X	X
Elasmopus rapax	X	
Erichthonius brasiliensis	X	X
Gitanopsis tortugae		X
Hemigena minuta		X
Lembos sp.		X
Listrella clymenella	X	X
Microprotopus raneyi		X
Monoculoides nyei	X	X
Orchestia platensis	X	
Protohaustorius sp.	X	X
Stenothoe minuta	X	X
Synchelidium sp.	X	X
Order Decapoda		
Albunea paretti		X
Alpheus sp.		X
Calappa sulcata		X
Callinectes sapidus	X	X
C. similis	X	X
Clibanarius vittatus	X	
Euceramus praelongus		X
Hepatus sp.		X
Hexapanopeus angustifrons	X	
H. paulensis		X
Isocheles wurdmanni	X	X
Labina dubia	X	
Latreutes fucorum	X	X
L. parvulus	X	X
Leptochela serratorbita		X
Metaporhapis calcarata		X
Neopanope texana		X
Ogyrides alphaerostris		X
O. limicola	X	X
Ovalipes guadulpensis	X	X
Paguridae	X	
Paguristes hummi		X
Pagurus longicarpus	X	
P. pollicaris	X	X
Penaeus aztecus	X	X
Persephona punctata		X
P. sp.		X
Petrochirus diogenes		X
Pinnixa cristata		X
P. sp.		X
Portunus gibbesi		X
Processa hemphilli		X
Sicyonia brevirostris		X
S. dorsalis		X
Trachypenaeus constrictus	X	X
Upogebia sp.		X
Xanthidae	X	

Table 3. Molluscan and crustacean biostandards from bay and offshore stations in faunal exchange analysis.

	Number	Rank
BAY STATION 3		
Mulinia lateralis (Say)	67	10
Nassarius vibex (Say)	14	9
Callinectes similis Williams	5	8
Ampelisca holmesi Pearse	4	6.5
Pagurus longicarpus Say	4	6.5
Ensis minor Dall	3	5
Penaeus aztecus Ives	2	4
Oxyurostylis smithi Calman	1	2
Clibanarius vittatus (Bosc)	1	2
Callinectes sapidus Rathbun	1	2
BAY STATION 4		
Mulinia lateralis (Say)	71	33
Callinectes similis Williams	69	32
Tellina iris Say	68	31
Synchelidium sp.	62	30
Pagurus longicarpus Say	56	29
Monoculoides nyei Shoemaker	54	28
Ampelisca holmesi Pearse	29	27
Anachis obesa Adams	13	26
Corophium acherusicum Costa	12	25
Latreutes parvulus (Stimpson)	11	24
Ovalipes guadulpensis (Saussure)	11	23
Hexapanopeus angustifrons (Benedict and Rathbun)	7	22
Nassarius vibex (Say)	5	21
Elasmopus rapax Costa	4	17
Acanthohaustorius sp.	4	17
Isocheles wurdmanni Stimpson	3	17
Mercenaria campechiensis (Gmelin)	3	17
Oxyurostylis smithi Calman	3	17
Trachypenaeus constrictus (Stimpson)	3	17
Pagurus pollicaris Say	3	17
Anadara transversa Say	2	10.5
Ancinus depressus (Say)	2	10.5
Erichthonius brasiliensis (Dana)	2	10.5
Stenothoe minuta Holmes	2	10.5
Protohaustorius sp.	2	10.5
Callinectes sapidus Rathbun	2	10.5
Donax tumidus Philippi	1	4
Terebra dislocata Say	1	4
Edotea montosa Stimpson	1	4
Libina dubia H. Milne Edwards	1	4
Squilla empusa Say	1	4
Anadara ovalis Bruguiere	1	4
Nassarius acutus (Say)	1	4

TABLE 3 continued.

BAY STATION 7, PRODUCING PLATFORM		
Mulinia lateralis (Say)	163	22
Ogyrides limicola Williams	73	21
Oxyurostylis smithi Calman	24	20
Macoma mitchilli Dall	18	19
Ensis minor Dall	17	18
Ampelisca holmesi Pearse	9	17
Batea catharinensis Muller	5	16
Eudorella monodon Calman	4	13.5
Ovalipes quadulpensis (Saussure)	4	13.5
Penaeus aztecus Ives	4	13.5
Callinectes similis Williams	4	13.5
Synchelidium sp.	3	11
Diplodonta punctata Say	2	7.5
Monoculoides nyei Shoemaker	2	7.5
Leucon sp.	2	7.5
Mercenaria campechiensis (Gmelin)	2	7.5
Stenothoe minuta Holmes	1	3.5
Cyclaspis sp.	1	3.5
Latreutes parvulus (Stimpson)	1	3.5
Docinus discus (Reeve)	1	3.5
Epitonium rupicola Kirtz	1	3.5
Polinices duplicata Say	1	3.5

BAY STATION 12, CONTROL		
Mulinia lateralis (Say)	315	16
Macoma mitchilli Dall	49	15
Nassarius vibex (Say)	18	14
Ogyrides limicola Williams	6	13
Nuculana concentrica Say	5	12
Eudorella mondon Calman	4	11
Oxyurostylis smithi Calman	3	9
Ampelisca holmesi Pearse	3	9
Paguridae	3	9
Thias haemostoma L.	2	7
Xanthidae	2	6
Orchestia platensis Kroyer	1	3
Callinectes similis Williams	1	3
Penaeus aztecus Ives	1	3
Listriella clymenella Mills	1	3
Batea catharinensis Muller	1	3

TABLE 3 continued.

OFFSHORE STATION 22A

Mulinia lateralis (Say)	3415	31
Synchelidium sp.	195	30
Monoculoides nyei Shoemaker	84	28
Trachypenaeus constrictus (Stimpson)	84	28
Tellina iris Say	84	28
Oxyurostylis smithi Calman	63	26
Latreutes parvulus (Stimpson)	23	25
Nassarius acutus (Say)	18	24
Nassarius vibex (Say)	17	23
Callinectes similis Williams	17	23
Ogyrides limicola Williams	17	23
Albunea paretti Guerin	14	21
Stenothoe minuta Holmesi	12	20
Penaeus aztecus Ives	10	18.5
Isocheles wurdmanni Stimpson	10	18.5
Protohaustorius sp.	9	17
Ancinus depressus (Say)	8	16
Polinices duplicatus Say	6	15
Corophium acherusicum Costa	5	14
Pagurus pollicaris Say	4	12.5
Persephona punctata Stimpson	4	12.5
Leptochela serratorbita Bate	3	10.5
Listrella clymenella Mills	3	10.5
Diplodonta punctata Say	2	7
Pinnixa cristata Rathbun	2	7
Oliva sayana Ravenel	2	7
Batea catharinensis Muller	2	7
Callinectes sapidus Rathbun	2	7
Caprella sp.	1	2.5
Edotea montosa (Stimpson)	1	2.5
Epitonium krebsi (Morch)	1	2.5
Anadara transversa Say	1	2.5

OFFSHORE STATION 30A

Corbula sp.	302	14
Anadara transversa Say	44	13
Diplodonta punctata Say	16	12
Nuculana concentrica Say	13	11
Nucula promixa Say	6	10
Sicyonia dorsalis Kingsley	3	9
Neotia ponderosa Say	2	7
Solen viridis Say	2	7
Mercenaria campechiensis (Gmelin)	2	7
Neopanope texana (Stimpson)	1	3
Tellina iris Say	1	3
Squilla empusa Say	1	3
Chione cancellata L.	1	3
Sinum perspectivum Say	1	3

TABLE 3 continued.

OFFSHORE STATION 17A, BENTHIC CONTROL #1		
Oxyurostylis smithi Calman	181	47
Monoculoides nyei Shoemaker	177	46
Stenothoe minuta Holmes	161	45
Synchelidium sp.	126	44
Lembos sp.	121	43
Erichthonius brasiliensis (Dana)	83	42
Latreutes parvulus (Stimpson)	72	41
Cyclaspis sp.	64	40
Leptochela serratorbita Bate	63	39
Gitanopsis tortugae Shoemaker	33	38
Euceramus praelongus Stimpson	27	37
Ovalipes guadulpensis (Saussure)	19	35
Albunea paretti Guerin	19	35
Processa hemphilli Manning and Chase	19	35
Paguristes hummi Wass	14	33
Nassarius acutus (Say)	13	31
Sicyonia dorsalis Kingsley	13	31
Hexapanopeus paulensis (Stimpson)	10	30
Cerapus tubularis (Say)	8	28
Hemigena minuta Mayer	8	28
Tellina iris Say	7	27
Trachypenaeus constrictus (Stimpson)	6	25
Ampelisca vadorum Mills	6	25
Portunus gibbesi (Stimpson)	6	25
Oliva sayana Ravenel	5	22.5
Diplodonta punctata (Say)	5	22.5
Sicyonia brevirostris Stimpson	4	20
Hexapanopeus angustifrons (Benedict and Rathbun)	4	20
Anadara transversa (Say)	4	20
Cantharus cancellarus (Conrad)	2	17.5
Neotia ponderosa (Say)	2	17.5
Munna sp.	1	8.5
Mulinia lateralis (Say)	1	8.5
Ogyrides alphaerostris (Kingsley)	1	8.5
Penaeus aztecus Ives	1	8.5
Alpheus sp. B	1	8.5
Metaphorhapis calcarata (Say)	1	8.5
Hepatus sp.	1	8.5
Petrochirus diogenes (L.)	1	8.5
Squilla empusa Say	1	8.5
Argopecten irradians (Lamarck)	1	8.5
Terebra dislocata Say	1	8.5
Turbonilla sp.	1	8.5
Anachis avara (Say)	1	8.5
Solen viridis Say	1	8.5
Murex fulvescens Sowerby	1	8.5
Chione grus (Holmes)	1	8.5

TABLE 3 continued.

OFFSHORE STATION 39A, BENTHIC CONTROL #2		
Latreutes parvulus (Stimpson)	154	27
Anadara transversa (Say)	47	26
Sicyonia dorsalis Kingsley	30	25
Trachypenaeus constrictus (Stimpson)	27	24
Euceramus praelongus Stimpson	18	23
Diplodonta punctata (Say)	16	22
Stenothoe minuta Holmes	15	21
Calappa sulcata Rathbun	8	20
Ampelisca vadorum Mills	7	18
Oxyurostylis smithi Calman	7	18
Sicyonia brevirostris Stimpson	7	18
Portunus gibbesi (Stimpson)	6	16
Hexapanopeus angustifrons (Benedict and Rathbun)	5	15
Leptochela serratorbita Bate	4	14
Erichthonius brasiliensis (Dana)	3	13
Synchelidium sp.	2	10.5
Hepatus sp.	2	10.5
Corbula sp.	2	10.5
Chione clenchi Pulley	2	10.5
Monoculoides nyei Shoemaker	1	4.5
Persephona (?) sp.	1	4.5
Nuculana concentrica Say	1	4.5
Argopecten irradians (Lamarck)	1	4.5
Noetia ponderosa (Say)	1	4.5
Squilla empusa Say	1	4.5
Processa hemphilli Manning and Chase	1	4.5
Oliva sayana Ravenel	1	4.5

Biomass

Data were sufficient to indicate a great variability in standing crop in the bay. Standard deviations were large, approaching or exceeding one-half the range at most stations (figures 2 and 3). Using analysis of variance methods to test bay biomass data, there were no significant differences between stations at one collecting period at the $F_{.1}$ level, but the spring biomass was significantly higher than other dates at the $F_{.05}$ level of significance.

Using a factorial analysis of variance, I tested offshore biomass data for differences in stations, dates, and station-date interaction. The most complete set of data was available from stations 35A, 17A, and 22A (figures 4 and 5). Dates, stations, and station-date interaction were all significantly different at the $F_{.005}$ level. By partitioning the degrees of freedom and sums of squares, I found station 22A to have a significantly higher biomass ($F_{.005}$) than stations 17A and 35A. The latter two stations

TABLE 3 continued.

OFFSHORE STATION 35A, PRODUCING PLATFORM		
Oxyurostylis smithi Calman	82	32
Synchelidium sp.	70	31
Latreutes parvulus (Stimpson)	68	30
Ampelisca vadorum Mills	50	29
Monoculoides nyei Shoemaker	36	28
Stenothoe minuta Holmes	33	27
Leptochela serratorbita Bate	19	26
Lembos sp.	16	25
Euceramus praelongus Stimpson	15	24
Processa hemphilli Manning and Chase	13	23
Sicyonia dorsalis Kingsley	10	22
Cyclaspis sp.	9	20.5
Diplodonta punctata (Say)	9	20.5
Gitanopsis tortugae Shoemaker	7	18.5
Tellina iris Say	7	18.5
Albunea paretti Guerin	6	16
Listriella clumenella Mills	6	16
Trachypenaeus constrictus (Stimpson)	6	16
Solen viridis Say	4	13.5
Portunus gibbesi (Stimpson)	4	13.5
Oliva sayana Ravenel	3	11
Alphaeus sp. A	3	11
Erichthonius brasiliensis (Dana)	3	11
Hexapanopeus angustifrons (Benedict and Rathbun)	2	8
H. paulensis Rathbun	2	8
Cantharus cancellarus (Conrad)	2	8
Noetia ponderosa (Say)	1	3.5
Paguristes hummi Wass	1	3.5
Sicyonia brevirostris Stimpson	1	3.5
Terebra dislocata Say	1	3.5
Ovalipes guadulpensis (Saussure)	1	3.5
Ampelisca holmesi Pearse	1	3.5

were then compared and while the stations were not significantly different in biomass, a difference in dates ($F_{.005}$) and date-station interaction ($F_{.05}$) was apparent.

Inspection of the data reveals consistent diminution in biomass values in the July 1973 sampling when the dissolved oxygen minimum was observed offshore. Comparison of values before and after July 1973 indicates that the drop in biomass was highly significant (at $F_{.005}$). The significant station-date interaction apparently results from station 17A being more severely affected by the O_2 minimum than station 35A.

Muddy stations were compared with 35A and 17A, and no significant difference was found between stations (at $F_{.1}$). Station 39A had a significantly greater biomass ($F_{.005}$) when compared with other

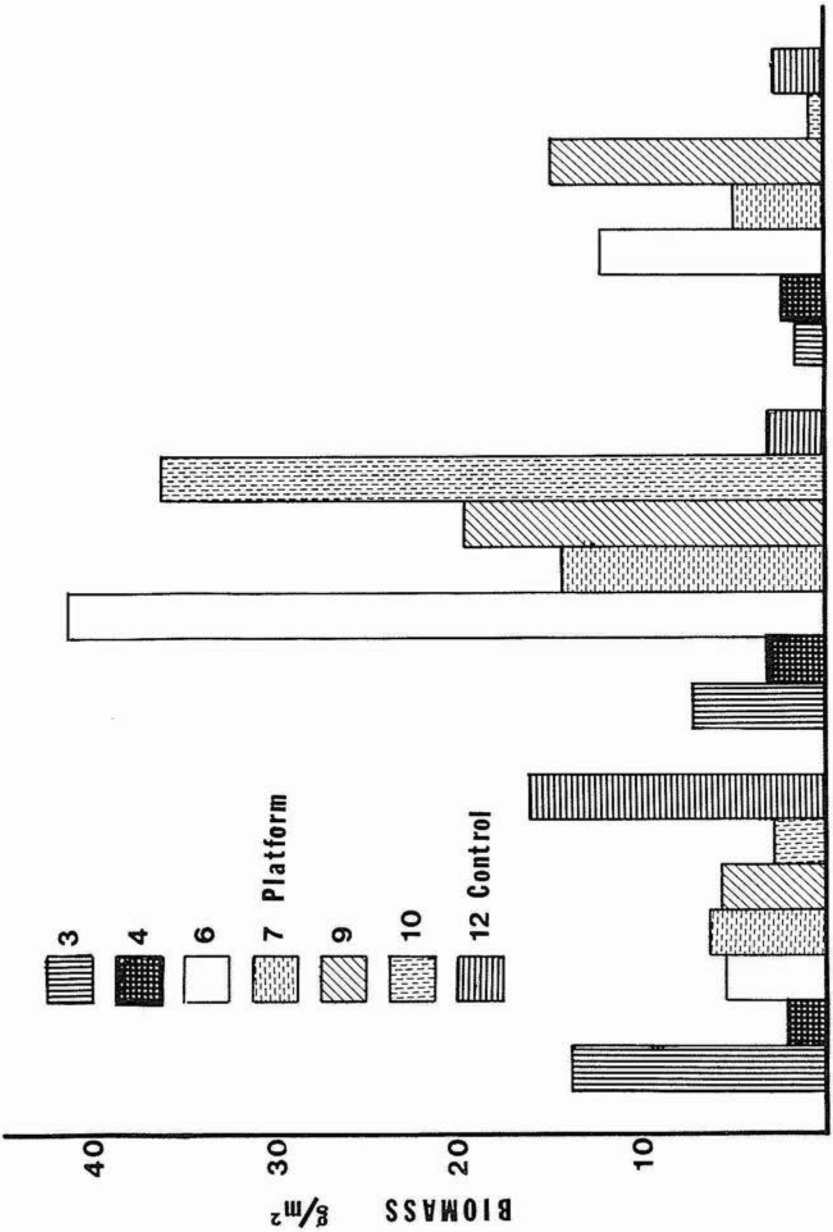

FIG. 2. BENTHIC BIOMASS FROM TIMBALIER BAY STATIONS, February 1973-July 1973.

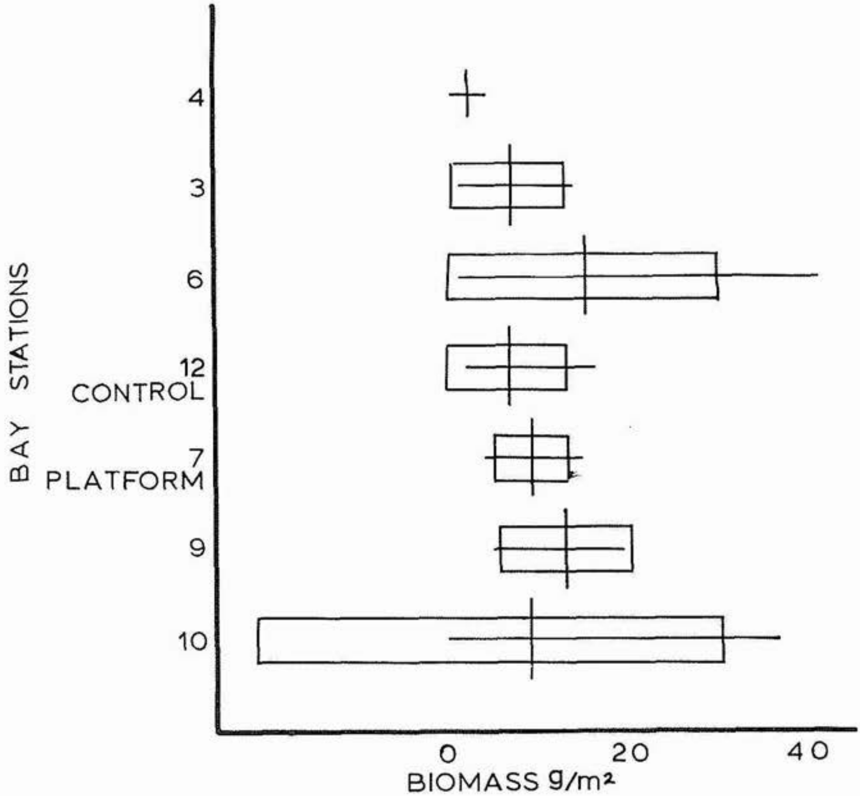

FIG. 3. TIMBALIER BAY BIOMASS DATA FROM TOTAL SAMPLES. Range indicated by horizontal line, mean indicated by vertical line, two standard deviations indicated by horizontal bar.

stations, but 39A was not sampled before the O_2 minimum and the effect on the station is unknown.

Faunal diversity and affinities

The Shannon-Weaver diversity index and Morisita index of similarity were used to analyze the molluscan and crustacean benthic communities. All benthic molluscs and crustaceans identified were used in the calculations. To eliminate sampling error and natural variation from calculation of index measurements, samples were pooled by station. Total Van Veen samples were combined for each station, and the SBT samples pooled. For faunal indices of offshore muddy substrates, station 30A was used, and separate calculations were included on total samples from all mud stations.

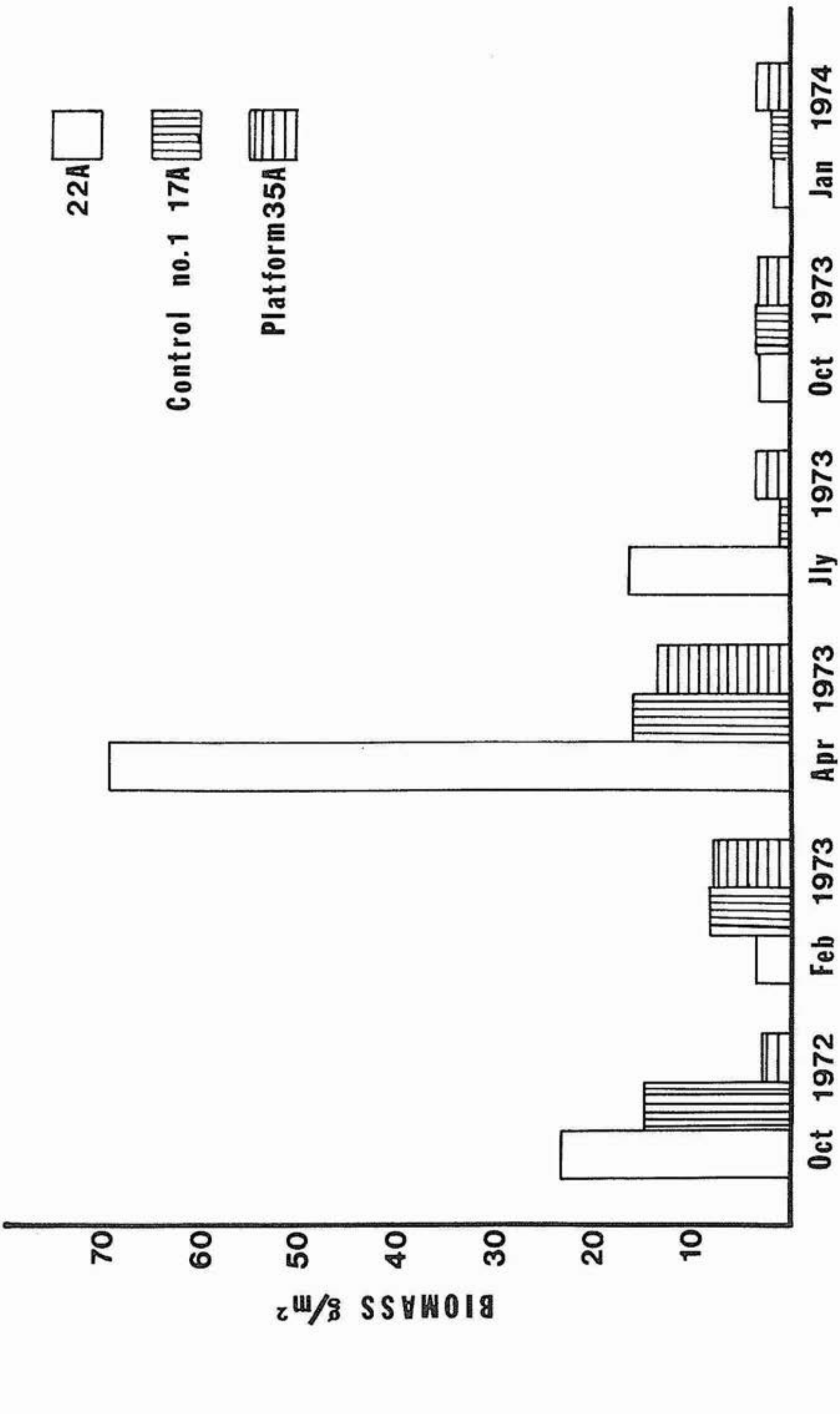

FIG. 4. BENTHIC BIOMASS FROM OFFSHORE STATIONS, October 1972-January 1974.

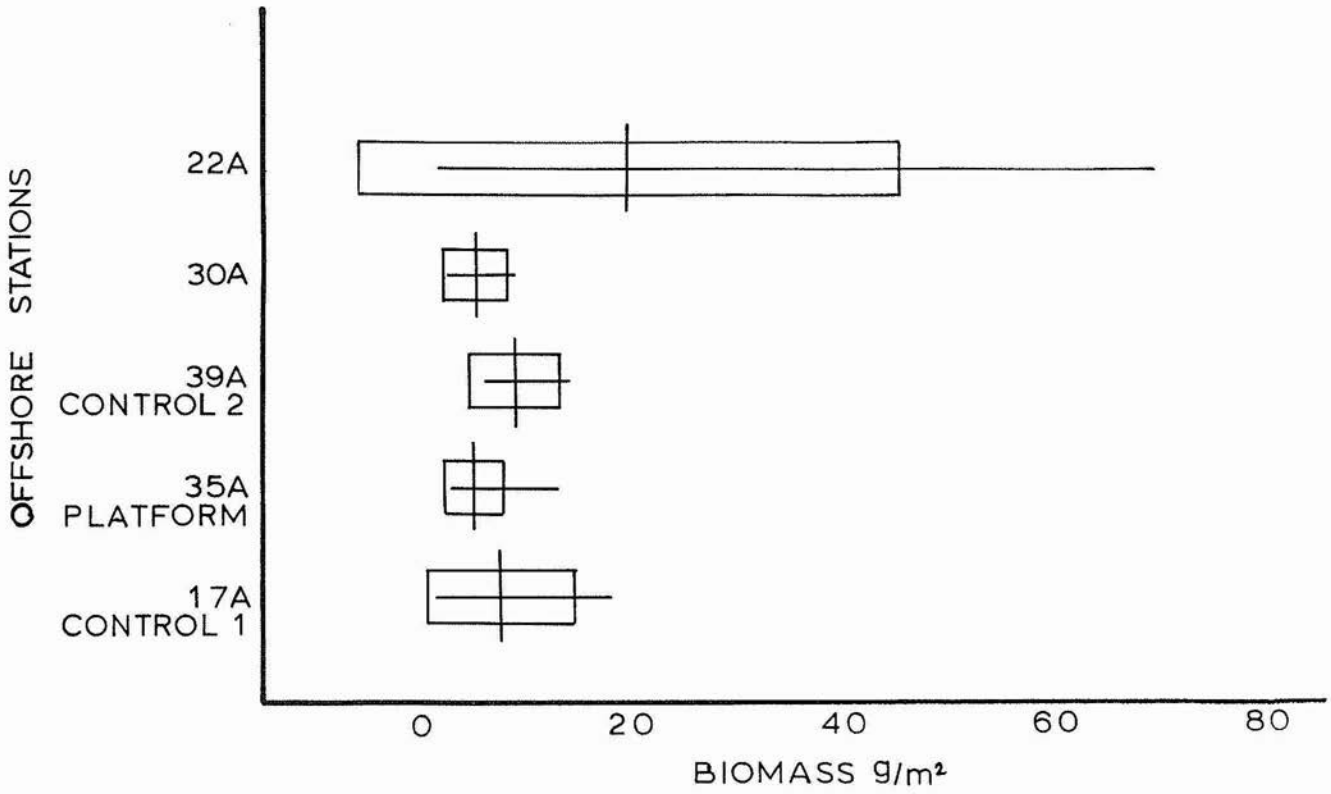

FIG. 5. OFFSHORE BIOMASS DATA FROM TOTAL SAMPLES. Range indicated by horizontal line, mean indicated by vertical line, two standard deviations indicated by horizontal bar.

Species diversity among bay Van Veen samples (table 4) was low (0.324-1.085), but overall diversity increased with increasing salinity (figure 6). The platform station was slightly more diverse (0.727) than the control (0.578). Diversity of SBT samples was higher than Van Veen samples, but, with the exception of station 4, species diversity remained relatively low. For SBT samples, diversity at the platform station (1.918) remained higher than the control (0.921). Evenness (J ') of bay Van Veen samples ranged from 0.26 to 0.52, and J ' of SBT samples ranged from 0.35 to 0.73. Another measure of diversity deals with distribution of biomass among taxa within a sample (figure 6). This measure of biomass diversity for bay stations ranged from 0.558 to 1.737, with values of 1.236 for platform station 7 and 1.031 for control station 12.

Diversity of near-shore stations (table 4) is relatively high at the platform and control site 1. Diversity of Van Veen samples was slightly higher at the platform (2.448) than at control 1 (2.340), and slightly lower at the platform (2.576 to 2.861) for SBT samples. Values from the second control were about 80% of the diversity of the platform, and diversity of station 22A (1.160 Van Veen, 0.861 SBT) was much lower than other offshore, sandy substrates. Values from muddy substrates were moderately low with Van Veen diversity of station 30A (0.947) exceeding SBT diversity (0.753); Van Veen diversity of pooled muddy stations (1.744) exceeded pooled SBT samples (0.849). Species equitability

Table 4. Species diversity for total Van Veen samples and total SBT samples. H'=sample diversity, H_{max}=Maximum possible diversity, J'=measure of species equitability.

Station Number	Van Veen Samples			SBT Samples		
	H'	H_{max}	J'	H'	H_{max}	J'
3	0.411	1.609	0.26	1.426	1.946	0.73
4	1.023	2.397	0.42	2.455	3.367	0.73
6	0.977	2.565	0.38	-	-	-
7 (Platform)	0.727	1.386	0.52	1.918	3.091	0.62
12 (Control)	0.578	1.386	0.42	0.921	2.639	0.35
9	0.5229	1.099	0.48	-	-	-
10	0.324	1.099	0.29	-	-	-
22A	1.160	3.044	0.38	0.923	2.398	0.39
30A	0.947	1.609	0.59	0.753	2.197	0.34
39A (Control #2)	1.899	2.302	0.82	2.066	3.091	0.67
35A (Platform)	2.448	2.996	0.82	2.576	3.296	0.78
17A (Control #1)	2.340	2.944	0.79	2.861	3.737	0.72
Muddy Substrates	1.744	2.485	0.70	0.849	2.773	0.31

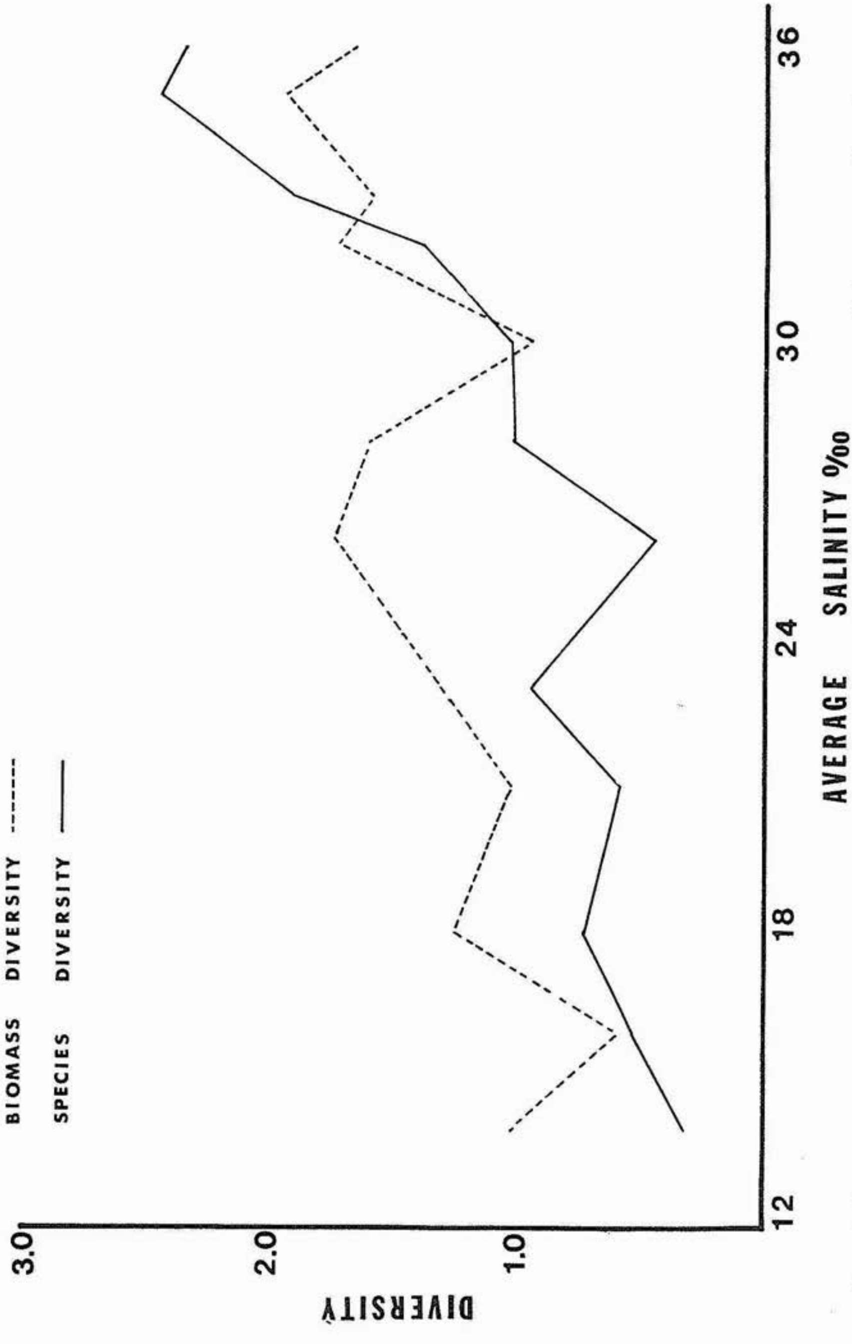

FIG. 6. SPECIES DIVERSITY AND BIOMASS DIVERSITY from Van Veen samples over salinity range of study area.

Table 5. Morisita-Ono index of faunal affinity values for total Van Veen samples.

Station No.	190	10	12 Control	9	7 Platform	6	3
4	.175	.003	.036	.036	.036	.050	.037
3	.001	.081	.987	.962	.953	.980	
6	.000	.085	.979	.965	.962		
7 Platform	.000	.078	.990	.996			
9	.000	.077	.975				
12 Control	.000	.081					
10	.000						

(J ′) values for offshore stations ranged from 0.38 to 0.82 for Van Veen samples and 0.26 to 0.78 for SBT samples. Biomass diversity from offshore stations ranged from 0.923 to 1.927 at the platform station to 1.629 at benthic control 1.

The general trends of species diversity and biomass diversity over the full salinity range of the study area are depicted by figure 6. With some variation, species diversity increased with increasing salinities. Biomass diversity does not appear to follow the same trend. Using analysis of variance to test for difference between bay and offshore diversities, I found no distinction between areas in biomass diversity, even at $F_{.1}$. Offshore, however, species diversity was significantly higher than bay diversity ($F_{.005}$).

Values for the Morisita index of faunal affinity range from 0.0 to about 1.0, with affinity between sample pairs increasing with increasing index values. Results of affinity calculations on bay Van Veen samples (table 5) indicate a very high correlation among stations 3, 6, 7, 9, and 12, index values ranging from 0.996 to 0.953 among these sampling sites. Stations 10, 4, and 190 showed little or no correlation to other stations or among themselves. Similarity of SBT samples follows the same trend as affinities of Van Veen samples (table 6).

Affinities among Van Veen samples were relatively low for the nearshore stations. The highest value was found between the platform station and control 1 (0.449), and the next highest between the platform and control 2 (0.350). These values were only a little lower than expected. Affinities among five replicate samples at station 17A varied from 0.59 to 1.00, indicating that distribution was not as homogeneous as that found at station 22, where agreement among replicate samples was

Table 6. Morisita index values for SBT stations from Bay and offshore Louisiana. Upper value from standard method, lower value, in parentheses, from nonparametric method.

Station No.	Offshore Control 17A	Offshore Platform 35A	39A	30A	22A	4	3	Bay Control 12
7 Bay Platform	.046 (.187)	.113 (.206)	.011 (.096)	.001 (.041)	.831 (.401)	.473 (.409	.854 (.606)	.355 (.896)
12 Bay Control	.008 (.105)	.013 (.105)	.002 (.049)	.001 (.139)	.902 (.507)	.355 (.381)	.890 (.687)	
3	.000 (.030)	.000 (.030)	.000 (.029)	.000 (.000)	.912 (.482)	.447 (.633)		
4	.378 (.354)	.380 (.350)	.086 (1.34)	.004 (.005)	.388 (.682)			
22A	.052 (.540)	.054 (.566)	.018 (.329)	.001 (.000)				
30A	.004 (.009)	.006 (.116)	.046 (.435)					
39A	.421 (.401)	.768 (.602)						
35A Offshore Platform	.9072 (.897)							

greater than 1.00. Affinity values from SBT samples indicate a high degree of faunal similarity between the platform station and control 1, and only moderate faunal affinity between the platform station and control 2. Among remaining stations, faunal relationship is low or nonexistent.

In addition to the standard Morisita index of faunal affinity, affinity values were calculated on the basis of species rank instead of number of individuals (table 6). Rank values were assigned to species in order of numerical dominance. When more than one species occurred with the same frequency, an average of the rank values was assigned. Because very large numbers of individuals at some stations may completely dominate the samples, the importance of some rarer species in transitional areas may be lost. If the species are ranked in order of numerical dominance, only the degree of domination is diminished. Using the rank value in the Morisita index results in a nonparametric application of faunal affinity. With this method, stations that agreed in most faunal components retained high affinity values. Station pairs that had high affinity values under the standard method, but were faunistically different except for one or two dominant species, had lower affinity values with the ranking method. Likewise, index values increased between station pairs with the same rarer species, but different dominant forms.

DISCUSSION

Maximum standing crop was observed during spring at most bay stations, and maximum density of molluscs and crustacean species occurred at this time. The lack of significant differences in biomass among various bay stations may be a function of low sample representation. However, while station 4 appeared lower than other stations in maximum observed biomass, this site did not exhibit the range of seasonal variation shown by other stations. This stability was the apparent reason that station 4 was not significantly different from other bay stations. Biomass of the offshore area apparently varies with seasons and depth. Highest biomass observed at any site (69 g/m^2) occurred in the muddy sand of the inner shelf (station 22A), and the clam *Mulinia lateralis* contributed over 90% of the weight. Since no significant differences were indicated among other stations sampled before the dissolved oxygen minima, substrate was apparently not a major factor in biomass distribution. Among stations sampled before July 1973, spring samples appear to represent biomass maxima.

Comparative biomass data from the northern Gulf of Mexico prior to this study were essentially nonexistent. I collected three Van Veen samples from medium sand in Mississippi Sound at a depth of 4 m, averaging 21.13 g/m^2. Gunter (1967) reported Petersen grab samples from "around the mouth of the Mississippi River" to have "drained" weights of 3.5 g from 3.5 to 4 fathoms and 0.8 g at depths greater than 4 fathoms. Fauchald (1971) found a standing crop off California of 300-800 g/m^2 in an echuroid worm (*Listhiolobus pelodes*) community in the vicinity of oil industry activity. Some fifteen years earlier, Barnard, Hartman, and Jones (1958) had reported biomass values up to 2,000 g/m^2 in the *Listhiolobus* community in the same area prior to the Santa Barbara oil spill of 1969. Since no benthic samples had been taken from this area, it is impossible to determine whether the decrease in biomass was the result of the oil spill or the result of natural variability of the benthic community. Barnard, Hartman, and Jones reported benthic biomass from several areas of the California shelf ranging from about 150 g/m^2 to about 400 g/m^2. Wigley and McIntyre (1964) studied the continental shelf off Massachusetts and found wet weights from 24.30 to 81.55 g/m^2 in depths of 40 to 58 m. By comparison, standing crop in Louisiana waters appears low, particularly for one of the most productive areas in the world.

Before species diversity is discussed, habitat diversity of the study area should be examined. The "level bottom" environment of Timbalier Bay and the adjacent shallow shelf varied in sediment type only from mud to fine sand; medium and coarse sand components were lacking. Except for shallow, isolated areas in the bay, there is no benthic flora, and little evidence of branching ectoprocts, sponges, or other sessile fauna. On the eastern side of the Mississippi River these floral and faunal components serve as habitat for numerous associated species. In Mississippi Sound, Farrell (1970) reported over 30 species of benthic amphipods, and total collections contained over 50 species. The present study includes only 16 benthic species. The amphipod components missing from Louisiana collections are largely those associated with either medium to coarse sand or benthic flora. Habitat diversity of the Louisiana substrate is low and can acount for low species diversity when compared with other areas. Shannon-Weaver diversity includes species richness and equitability as factors in the calculated diversity value. The species equitability measure "J" was low for most bay stations and the shallowest offshore stations, indicating an oligomixic community numerically dominated by one or two species.

Use of species diversity as a means of detecting pollution in aquatic environments has been demonstrated as an effective and sensitive method (Wilhm 1972; Wilhm and Dorris 1966, 1968; Boesch 1972, 1973). The assumption is made that more sensitive fauna will be reduced or eliminated from the area of abnormal stress. Lower species diversity values of the community reflect the loss of species.

Within the scope of this study, there were no significant differences between the bay platform station and the other central bay stations in standing crop or species diversity. As a result of the July 1973 oxygen minima, the offshore situation was not as clear cut. However, present data indicate that there were no real differences in biomass or standing crop between the platform and offshore control 1. In both the bay and offshore areas, there was no indication of long-term detrimental effects on the benthos by oil industry activity.

Dissolved Oxygen Minima

The exact cause of the dissolved oxygen minima is a matter of speculation. Brongersma-Sanders (1957), in a survey of mass mortality at sea, includes lack of oxygen in isolated bottom water and in association with noxious waterbloom among known causes for marine fish kills. During the summer months the envelope of bottom water on the Louisiana shelf was isolated; a source of eutrophication was present in the abnormally high flood of the Mississippi River; and high phaeopigments were reported during July near the bottom by investigators studying primary productivity (El Sayed 1974). From the evidence at hand, I believe that the offshore Louisiana oxygen minima resulted from high respiration and high BOD from mortality of an abnormally large phytoplankton bloom. The high phaeopigment level during July sampling tends to support this contention. Of course, mortality of benthic species would only contribute to the BOD. Whatever the cause, the oxygen minima were the most important stress factor on offshore benthos during the sampling phase of this study.

Community relationships

Carriker (1967) reviews various arguments concerning reality of benthic biocoenosis as a biological unit and applications to estuaries, and points out that an estuary is not simply an area of integration between fresh and salt water, but possesses unique faunal components. Whether an estuary is represented by a single community divided into a series of sub-communities (Barnard 1970) or a series of communities contributing to a major faunal zone is a matter of semantics. Throughout the Louisiana Bay and offshore study area, several changes in substrate were evident, as well as the gradient in salinity. From a standpoint of salinity ranges, the entire study area would have to be classified as estuarine. Even the most saline station (17A) ranged from 31.4-36.1 ppt. For simplicity the various ecological units in this study were considered benthic communities.

None of the Louisiana sampling sites could be characterized by a molluscan or crustacean species throughout the entire sampling phase.

Biocoenoses in this study appear to have a dynamic stability in which dominance of principal species is probably cyclic. Exceptions would be expected in the event of abnormal stress, such as the DO minima in the near-shore region. Fauna best able to cope with low oxygen levels would have a survival advantage, and dominance would shift.

Another factor to be considered in examining communities is continua of distribution. Mills (1971) observed that different benthic species that have population maxima at the same site may have radically different distribution patterns. During this study several euryhaline crustacea were found ranging from the bay to sandy offshore stations where apparent population maxima occurred. These crustaceans were among the numerically dominant fauna at control site 1 (17A) and the platform station, but were sufficiently eurybiotic to span other biotopes.

Examination of physical parameters of all stations in the bay and near-shore regions shows two distinct biotopes within each region and a transitional area in the vicinity of the bay mouth (figure 7):

1. Mesohaline bay, muddy substrate, minimum temperature below 15° C, low energy;
2. Polyhaline bay, sandy mud substrate, minimum temperature below 15° C, low energy;
3. Polyhaline bay mouth (transitional area), fine sand-muddy sand substrate, minimum temperature below 15° C, moderate energy;
4. Euryhaline near-shore, sandy mud-mud substrate, minimum temperature about 15° C, low energy;
5. Euryhaline near-shore, muddy sand-sand substrate, minimum temperature above 15° C, low energy.

The standard Morisita-Ono index of faunal affinity applied to samples throughout the study area helps define the real biotopes and evaluate interchange among stations. Station 10 in Little Lake was dominated by the clam *Macoma mitchilli* at spring sampling, and showed only minor exchange with any other stations. Central Bay stations 6, 7, 9, and 12 all have very high faunal similarity when examined on the basis of total Van Veen samples. All show, more or less, a biocoenosis of oligomixity with domination by the pelecypod *Mulinia lateralis*. Composition of less abundant species differed among some stations, but the pelecypod *Macoma mitchilli*, decapod *Ogyrides limicola*, amphipod *Ampelisca holmesi*, and the cumaceans *Oxyurostylis smithi* and *Eudorella mondon* were among the most common species from the area.

Station 3 agrees with the central bay in dominance of *M. lateralis* but differs in less abundant species. Station 3 was located on sand flats

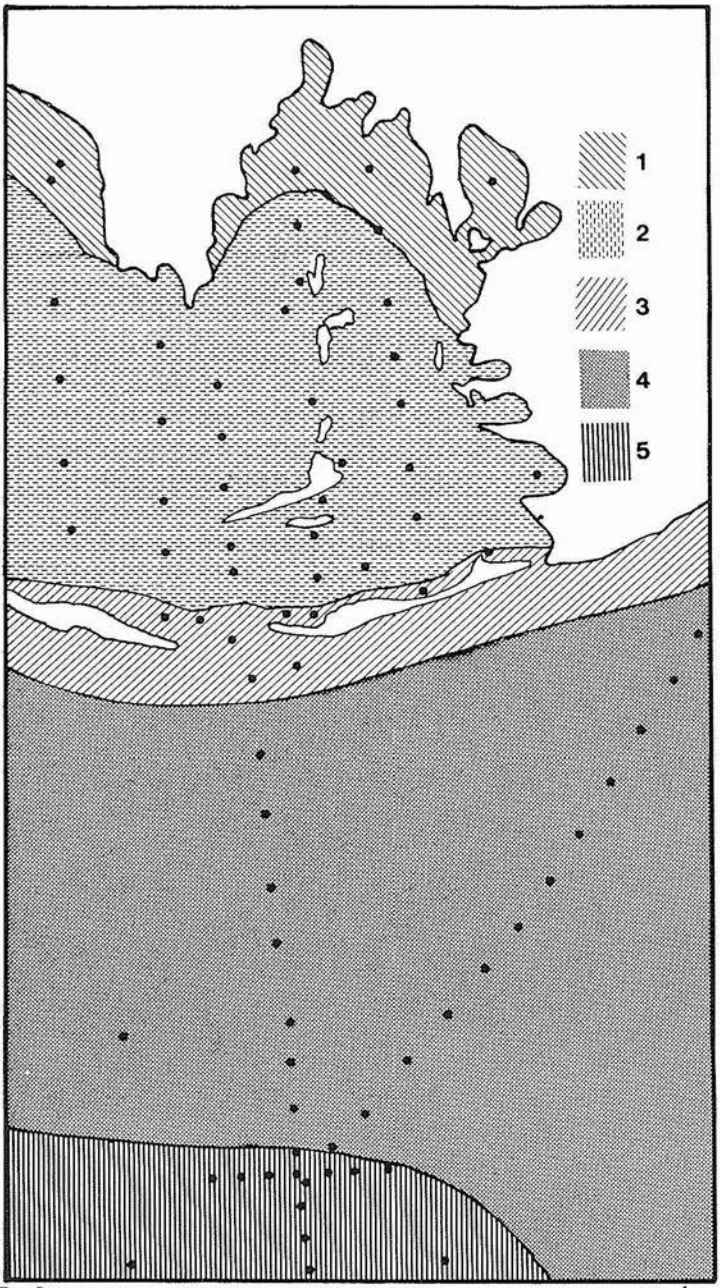

FIG. 7. IDEALIZED BIOTOPE DISTRIBUTION OF STUDY AREA based on general physical parameters. 1 - mesohaline Bay; 2 - polyhaline Bay, sandy mud substrate; 3 - polyhaline transitional area, sand substrate; 4 - euryhaline offshore, sandy mud substrates; 5 - euryhaline offshore, sandy substrate. Points represent locations of data acquisition.

along the inside of E. Timbalier Island. It was more comparable, ecologically, to station 4 than to other stations in the bay. Station 4 near the pass into Timbalier Bay represents the transition area, exemplified by low to medium low affinities in comparison to all other stations. Diversity is relatively high, because there is no clear-cut dominance. The clams *Tellina iris* and *Mulinia lateralis,* amphipods *Synchelidium* sp. and *Monoculoides nyei,* and decapods *Pagurus longicarpus* and *Callinectes similis* were equally abundant. Rather than just representing range extremes of bay or offshore species, station 4 fauna is largely euryhaline and estuarine species that are represented in both offshore and bay samples. Also included are several apparent endemic forms that probably prefer the higher energy environment.

Despite the location on the shallow shelf, station 22A had very high affinities with the central bay stations and no real correlation with other offshore sites with the standard Morisita index. *Mulinia lateralis* reached its apparent population peak at this station, and on the basis of this species station 22A would be lumped into the bay biocoenosis. Inspection of species components showed that station 22A is really a transition station and represents the range extremity of many offshore and bay species. The Morisita index, using species rank, indicates that similarity to other offshore stations was equal to bay stations if dominance of *M. lateralis* was reduced.

Stations 35A, 17A, and 39A are offshore sites with sand to muddy sand substrates and less variability among the physical parameters. The cumacean *Oxyurostylis smithi*; amphipods *Synchelidium* sp., *Monoculoides nyei,* and *Stenothoe minuta*; and the caridean shrimp *Latreutes parvulus* and *Leptochela serratorbita* were the dominant species in this area.

Between the deep stations, which are characterized by sand substrate, and the shallow shelf lies a distinct mud-sandy mud biotope represented by stations 21A, 28A, and 30A. Since SBT data are available from station 30A, this site was used to represent offshore muddy bottom communities. The dominant species, *Corbula* sp. (Pelecypoda), was encountered only rarely in other biotopes.

As was previously mentioned, both standard and nonparametric application of the affinity index were used to test similarity among SBT stations throughout the study area. Values between station-pairs were different only when the stations agreed in one or two dominant species but did not agree in the majority of the less common species. To depict faunal exchange between a bay station and other sites, platform station 7 was selected, since it was the most brackish SBT sampling site (figure 8). With the ranked Morisita index, station 7 shows high similarity only to station 12, moderately high affinity with bay station 4 and shallow shelf

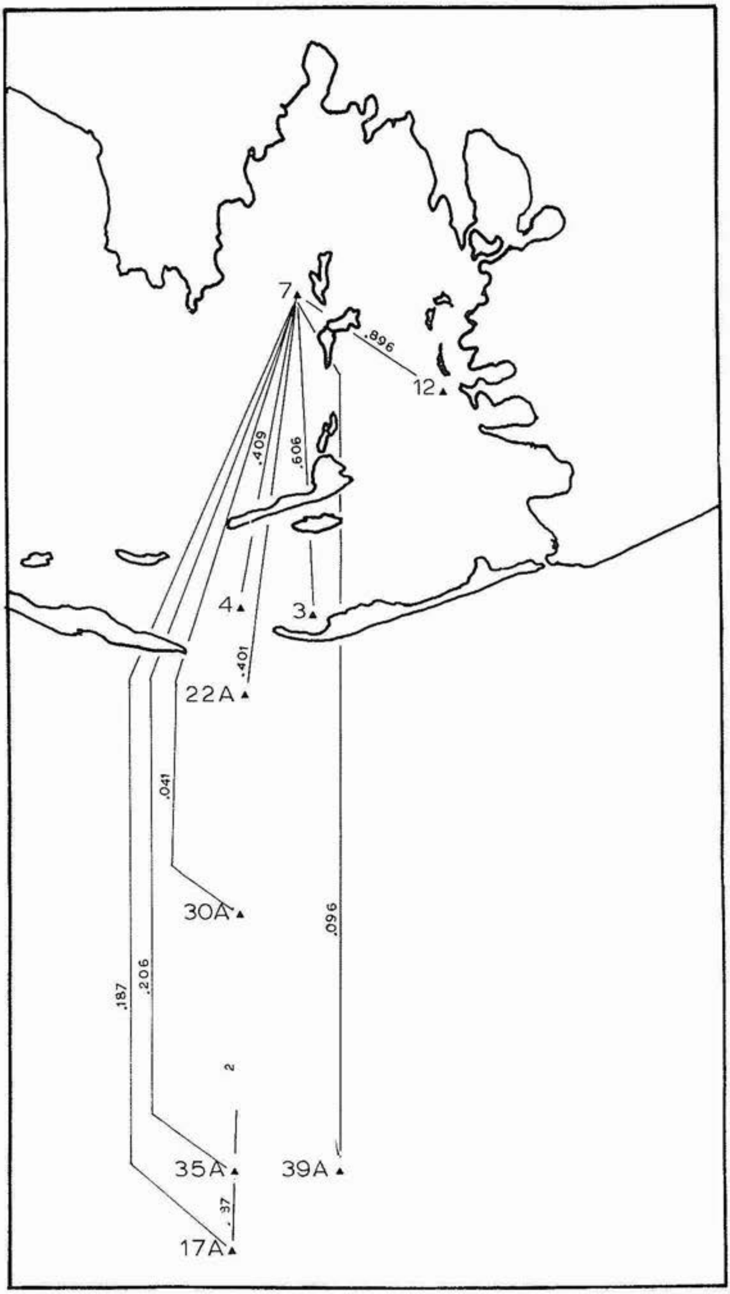

FIG. 8. NONPARAMETRIC FAUNAL AFFINITY between bay station 7 and other SBT stations within the study area.

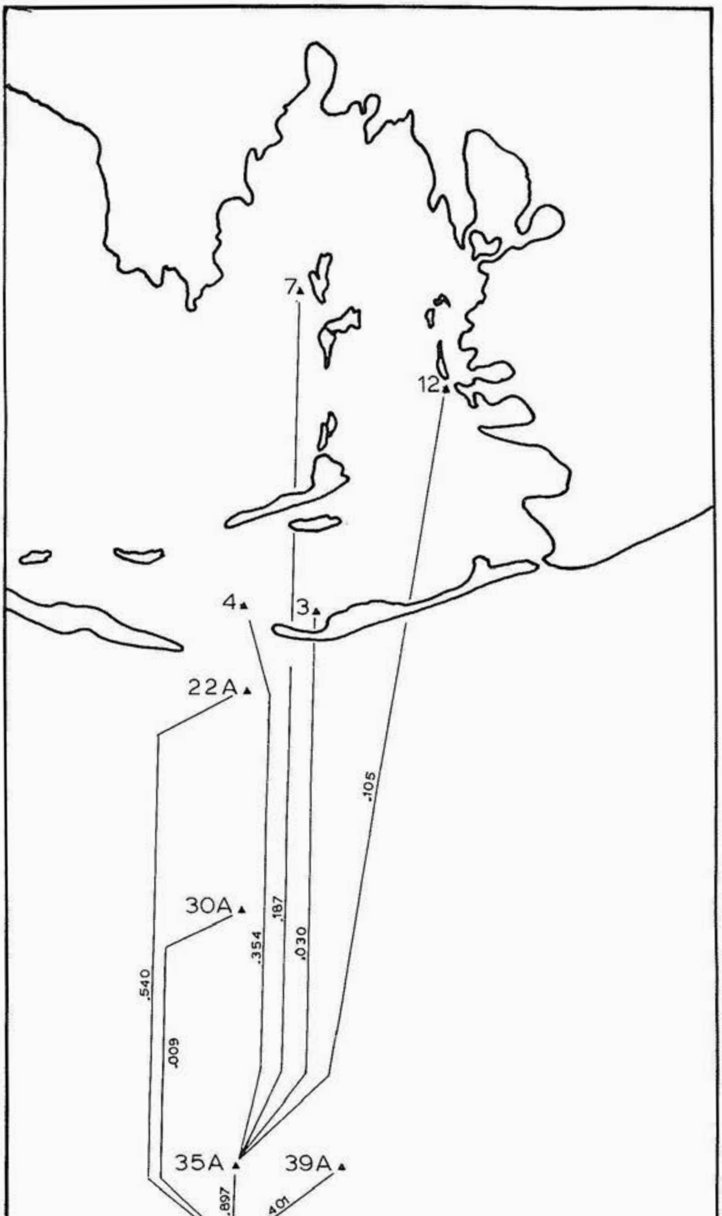

FIG. 9. NONPARAMETRIC FAUNAL AFFINITY between offshore station 17A and other SBT stations within the study area.

site 22A, low affinity to the deep sandy substrates, and no similarity to the offshore muddy bottoms.

For offshore stations, control 1 (17A) was selected for comparison with other stations because this site was the most saline and the most distant from shore (figure 9). Station 17A showed a high affinity with station 35A, a moderate affinity with offshore stations 39A and 22A, and a low affinity with station 4 at the mouth of the bay.

Despite the fact that salinity ranges and species composition indicated that the entire area was estuarine, the sampling area can be divided into two major faunal zones, bay and offshore, with at least two biocoenoses in each zone. The area in the vicinity of East Timbalier Pass could be called a fifth or transitional community. To gain further insight into species exchange between the zones, the various species were categorized according to estuarine habitat (figure 10). Migrants, largely commercial shrimp and crabs, included only a few species and ranged

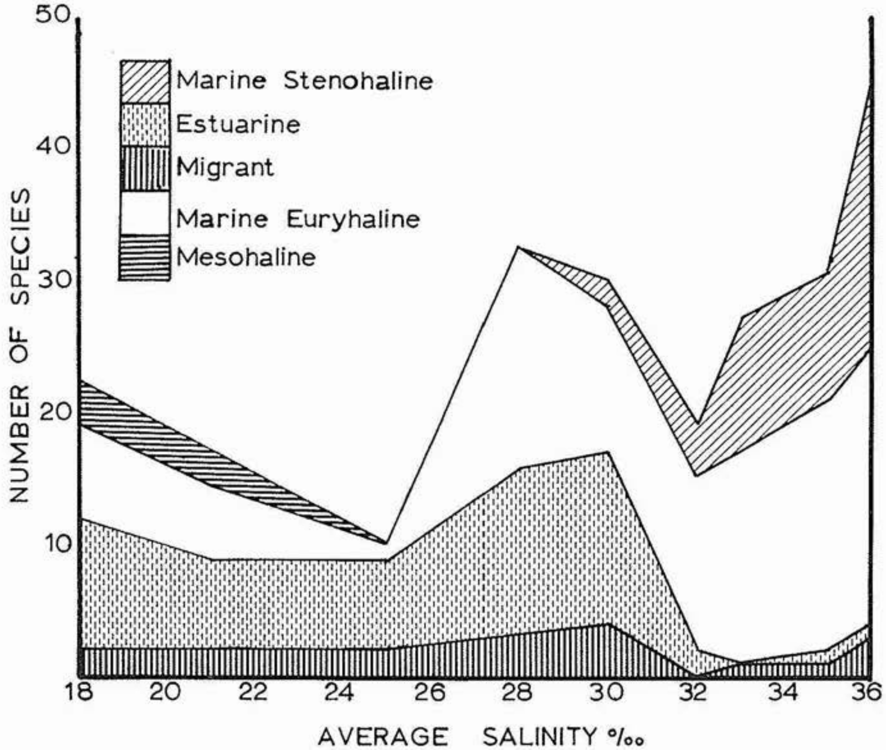

FIG. 10. CUMULATIVE NUMBER OF SPECIES for SBT stations, species classified by ecological habitat.

over the entire sampling area. Mesohaline species were not collected beyond bay stations 7 and 12, and the remaining bay fauna (estuarine species) barely ranged beyond the transition area, offshore station 22A. The low, but distinct, faunal affinity between the deeper offshore areas and bay stations 7 and 12 resulted from invasion of marine euryhaline species—pelecypod, *Diplodonta punctata*; cumaceans, *Oxyurostylis smithi* and *Cyclaspis* sp.; amphipods, *Monoculoides nyei*, *Synchelidium* sp., and *Stenothoe minuta*; and the decapod *Latreutes parvulus*.

While the effect of substrate on species distribution was pronounced on the shelf, bottom type was apparently not as critical in the bay. For example, the fossorial amphipods, *Synchelidium* sp. and *Monoculoides nyei*, were limited entirely to sandy substrates at offshore stations, but in Timbalier Bay they were collected in substrates ranging from sand to sandy mud. McLusky (1968) found that local distribution of the amphipod *Corophium volutator* was substrate-dependent within its optimal salinity range, but in more brackish water, salinity was the factor controlling distribution. Similar factors may have contributed to spatial distribution of marine euryhaline species in Timbalier Bay.

ACKNOWLEDGMENTS

I wish to thank Dr. Robert Menzies for his guidance throughout the duration of this project. Thanks are also due Drs. Jim Jones, Ruby Krishnamurti, and Winston Menzel of the Oceanography Department of the University of Florida for their invaluable advice, and Drs. Van Belle and Metter for assistance with statistical aspects of this problem. Drs. James Marum, Allen Paul, and Robert Avent contributed much help through lengthy discussions and constructive criticism. This project was funded by the Gulf Universities Research Consortium, Contract No. OB69JM, and was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

REFERENCES CITED

Barnard, J. Laurens. 1970. Benthic ecology of Bahia de San Quintin, Baja California. Smithsonian Contributions to Zoology, No. 44.

———, O. Hartman, and G. F. Jones. 1958. Benthic biology of the mainland shelf of southern California. *In* Oceanographic Survey of the Continental Shelf Area of Southern California. Allan Hancock Foundation, University of Southern California, pp. 265-430.

Barrett, B. B., J. W. Tarver, W. R. Latapie, J. F. Pollard, W. R. Mock, G. B. Adkins, W. J. Gaidry, C. J. White, and J. S. Mathis. 1971a. Phase 2, hydrology. *In* W. S. Perret, Coordinator, Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana. Louisiana Wildlife and Fisheries Commission.

———. 1971b. Phase 3, sedimentology. *In* W. S. Perret, Coordinator, Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana. Louisiana Wildlife and Fisheries Commission.

Basharin, G. P. 1959. On a statistical estimate for the entropy of a sequence of independent random variables. Theory of Probability and its Applications **4**:333-336.

Behre, E. H. 1950. Annotated list of the fauna of the Grand Isle region. Occasional Papers, Marine Laboratory, Louisiana State University **6**:1-66.

Boesch, D. F. 1972. Species diversity of marine macrobenthos in the Virginia area. Chesapeake Science **13**(3):206-211.

———. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Marine Biology **21**:226-244.

Brongersma-Sanders, M. 1957. Mass mortality in the sea. *In* J. W. Hedgpeth, ed., Treatise on Marine Ecology and Paleoecology. Vol. I, pp. 941-1010. Geological Society of America Memo **67**.

Carriker, Melbourne R. 1967. Ecology of estuarine benthic invertebrates: a perspective. *In* George R. Lauff, ed., Estuaries. No. 83, American Association for the Advancement of Science, pp. 442-487.

Causey, D. 1953. Parasitic Copepoda from Grand Isle, Louisiana. Occasional Papers, Marine Laboratory, Louisiana State University **7**:1-18.

Christmas, J. Y., ed. 1973. Cooperative Gulf of Mexico estuarine inventory and study, Mississippi. Gulf Coast Research Laboratory, State of Mississippi.

Dawson, C. E. 1966. Additions to known marine fauna of Grand Isle, Louisiana. Proceedings, Louisiana Academy of Science **21**:175-180.

Deichmann, E. 1946. A new species of *Thyone* s.s. from the Gulf of Mexico *Thyone mexicana* sp. nov. Occasional Papers, Marine Laboratory, Louisiana State University **4**:1-4.

El-Sayed, S. Z. 1974. Effect of oil production on the ecology of phytoplankton off the Louisiana coast. Gulf Universities Research Consortium. Appendix to Report No. 138.

Farrell, D. H. 1970. Ecology and seasonal abundance of littoral amphipods from Mississippi. Unpublished M.S. thesis, Mississippi State University.

Fauchald, K. 1971. Benthic fauna in Santa Barbara channel following the January 1969 oil spill. *In* Dale Straughan, ed., Biological and Oceanographic Survey of Santa Barbara Channel Oil Spill, Vol. 1. University of Southern California.

Griffin, G. M. and B. S. Ripy. 1974. Turbidity, suspended sediment concentrations, clay mineralogy of suspended sediments, and the origin of the turbid near-bottom water layer—Louisiana shelf south of Timbalier Bay—August 1972-January 1974—with comments on a process model for turbid layer transport. Gulf Universities Research Consortium. Appendix to Report No. 138.

Gunter, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. *In* George H. Lauff, ed., Estuaries. No. 83, American Association for the Advancement of Science, pp. 621-638.

Harry, H. W. 1942. List of Mollusca of Grand Isle, Louisiana, recorded from the Louisiana State University Marine Laboratory 1929-1941. Occasional Papers, Marine Laboratory, Louisiana State University **1**:1-13.

Hoff, C. C. 1943. The description of a new ostracod of the genus *Potamocypris* from Grand Isle, Louisiana, and records of ostracods from Mississippi and Louisiana. Occasional Papers, Marine Laboratory, Louisiana State University **3**:1-11.

McHugh, J. L. 1966. Management of estuarine fisheries. American Fishery Society Publication **3**:133-154.

McLusky, D. S. 1968. Some effects of salinity on distribution and abundance of

Corophium volutator in the Ythan estuary. Journal of the Marine Biological Association, U.K. **48**:442-454.

Mills, E. L. 1971. Views of the community concept, with comments on continua and the role of instability in some marine benthic communities. Vie et Milieu, Troisième Symposium Europeen de Biologie Marine. Supp. **22**:145-153.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E **3**:65-80.

Parker, Robert H. 1956. Macroinvertebrate assemblages as indicators of sedimentary environments in east Mississippi delta region. American Association of Petroleum Geologists Bulletin **40**(2):295-376.

———. 1960. Ecology and distributional patterns of marine macroinvertebrates, northern Gulf of Mexico. Recent Sediments, Northwest Gulf of Mexico, 1951-1958. Tulsa, Oklahoma: American Association of Petroleum Geologists.

Perret, W. S., W. R. Latapie, J. F. Pollard, W. R. Mock, G. B. Adkins, W. J. Gaidry, and C. J. White. 1971a. Phase I, area description. *In* W. S. Perret, Coordinator, Comparative Gulf of Mexico Estuarine Inventory and Study, Louisiana. New Orleans: Louisiana Wildlife and Fisheries Commission, pp. 3-27.

———. 1971b. Fishes and invertebrates collected in trawl and seine samples in Louisiana estuaries, phase 4, sec. 1. *In* W. S. Perret, Coordinator, Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana. New Orleans: Louisiana Wildlife and Fisheries Commission, pp. 41-105.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology **13**:131-144.

Rounsefell, G. A. 1966. Realism in the management of estuaries. Marine Research Bulletin **1**:1-13.

St. Amant, L. S. 1971. Impact of oil on the Gulf Coast. Transactions of the Thirty-Sixth North American Wildlife and Natural Resources Conference, pp. 206-219.

———. 1972. The petroleum industry as it affects marine and estuarine ecology. Journal of Petroleum Technology **24**(4):385-392.

Shannon, C. E. and W. Weaver. 1963. The Mathematical Theory of Communication. Urbana: University of Illinois Press.

Sprague, V. 1950. Notes on three Microsporidian parasites of Decapod Crustacea of Louisiana coastal waters. Occasional Papers, Marine Laboratory, Louisiana State University **5**:1-8.

Waldron, Robert P. 1963. A seasonal ecological study of Foraminifera from Timbalier Bay, Louisiana. Gulf Research Reports **1**(4):132-188.

Wigley, R. L. and A. D. McIntyre. 1964. Some quantitative comparisons of offshore meriobenthos and macrobenthos south of Martha's Vineyard. Limnology and Oceanography **9**:483-493.

Wilhm, J. L. 1967. Use of biomass units in Shannon's formula. Ecology **49**(1):153-156.

———. 1972. Graphic and mathematical analyses of biotic communities in polluted streams. Annual Review of Entomology **17**:223-252.

——— and T. C. Dorris. 1966. Species diversity of benthic macroinvertebrates in a stream receiving domestic and oil refinery effluents. American Midland Naturalist **76**(2):427-449.

——— and T. C. Dorris. 1968. Biological parameters for water quality criteria. Bioscience **18**(6):477-481.

Willis, E. R. 1942. Some mud shrimps of the Louisiana coast. Occasional Papers, Marine Laboratory, Louisiana State University **2**:1-6.